

XXXIII.—*On the Classificatory Value of Growth and Budding in the Madreporidæ, and on a new Genus illustrating this point.* By STUART O. RIDLEY, M.A., F.L.S., &c., Assistant in the British Museum (Natural History).

[Plate XI.]

THE manner in which growth is effected in the corallum has long been considered a character of very great importance for the systematic division of the Madreporaria.

Thus MM. Milne-Edwards and Haime (Hist. Nat. Corall.) appeal constantly to the characters gemmiparity and fissiparity, and the various modifications of gemmiparity, in the formation of their genera, and (*e.g.* Astrangiaceæ, Oculinidæ) sometimes in the distinction of larger groups; they point out at the same time that gemmiparity may occur in a group (Turbinoliidæ) whose members are not normally compound.

In the genus *Madrepora* the characteristic form of increase has been held by the highest authorities to be that of lateral extracallicinal gemmation from a primary zooid. Thus Ehrenberg (Cor. roth. Meer. p. 108) defines that section of his family Madreporina which he calls *Heteropora*, but which is now termed *Madrepora*, as follows:—"Stella ramulorum qualibet solitaria, gemmipara, sæpe maiore (gubernatrice), reliquis raro gemmiparis, minoribus (frutices erectos, ramosissimos, prostratosve formant)."

Dana's generic diagnosis of *Madrepora* (U.S. Expl. Exp. Zool. p. 431) is:—"Patrio-ramose; arborescent, caespitose, or, through coalescence, reticulate or foliaceous. Coralla with the branches terete (very rarely compressed); calicles regular." He says further, "The genus *Madrepora* includes species which bud from a parent-polyp, with which each branch terminates. . . . But two or three species are known in which the apical polyp cannot be distinguished; and these form a connecting-link between this genus and the following" (the following genus is *Manopora*, Dana, = *Montipora*, De Blainville). The three species mentioned by Dana as not having an apical polyp are *M. cuneata*, *labrosa*, *securis*.

Milne-Edwards and Haime (Hist. Nat. des Coralliaires, p. 132) define *Madrepora* thus:—"Polypierites réunis en masses ramifiées, fasciculées ou lobées. Calices saillants, au moins dans le jeune âge, à ouverture petite ou médiocre et à bords assez épais. Cloisons non débordantes. Columelle nulle;" and continue, pointing out that budding is usually circular and that "le polypierite souche de chaque pousse est

presque toujours plus développé que ceux dont il est entouré et constitue à l'extrémité de chaque branche ou ramuscule, un calice dit apical, qui est plus grand et plus proéminent que les calices latéraux."

Verrill ("Review of the Corals and Polypes of the West Coast of America," Trans. Connecticut Acad. i. (1869) p. 501) says of *Madrepora* and *Montipora*, "The resemblance between certain species of these two genera, both in appearance and structure, is very close, the chief difference being that in *Madrepora* there is usually a terminal or leading polyp at the end of each branch, which is not the case in *Montipora*." Klunzinger (Korallenthier der rothen Meeres, ii. p. 2) commences his account of *Madrepora* by stating that "the colony bears branches which are usually more or less round, and the terminal calicle of which is always distinguished by size or shape from the numerous lateral calicles which lie as lateral buds around the median calicle." Studer (Monatsbericht Akad. wiss. Berlin, 1878, p. 535) does not define *Madrepora*; but at the end of his account of those species of the genus collected by the 'Gazelle' establishes a new subgenus, which he calls *Isopora*, and defines as "Cormus foliar or lobate, the calicles projecting equally, distributed evenly over the whole colony, no specially differentiated apical calicle," placing under it *Madrepora securis* and *labrosa* of Dana. [In view of the unwieldiness of the large genus *Madrepora*, it is perhaps desirable that it should be thus subdivided for working purposes in this way into minor groups or subgenera, and perhaps *M. elegans* might advantageously be similarly set aside from the rest of the genus, as suggested by Milne-Edwards and Haime (*l. c.*.)] Subsequently (see below, *ad fin.*) Studer suggests fission or marginal gemmation as the mode of growth in *Madrepora*.

Now it seems to me that while these various accounts of the distinctive characters of *Madrepora* as opposed to *Montipora* lay sufficient weight on the external facts of this distinction, they do not, as a rule, bring forward the underlying law of which these facts (*i. e.* the terminality or non-terminality of the distal calicles) are merely an expression, viz. the character of the budding, which is essentially and fundamentally diverse in the two cases.

To how great an extent this essential difference has been overlooked seems to be strikingly shown by Dana's remark above quoted, to the effect that the species of *Madrepora* without an apical calicle "form the connecting-link between this genus" (*Madrepora*) "and the following" (*Montipora*). This assertion does not even find support in the

evidence he adduces, viz. the growth of these species in erect or incrusting plates, and the absence of an apical polype, for the simple fact is, that, though in the species referred to there is no *one* apical polype, there are instead *several*. I have examined two of these species, *labrosa* and *cuneata*, and find that the ends of the branches are well covered by large calices, at the sides (and in *cuneata*, at any rate, *from* the sides) of which originate young calices. The fact that there is no *one* apical calicle appears to be due to the fact that on the broad ends of the lobes all calices are equally circumstanced, whereas in the pointed-ended *Madreporæ* the terminal calicles stand alone in position and circumstances.

In point of fact the most essential distinction between *Madrepora* and *Montipora* is thus overlooked by Dana. In *Madrepora* (as may be seen at once by examining the ends of branches of any species except *labrosa*, *securis*, *cuneata*) one or more calices take the lead in the growth, and others originate *below* them, constituting a *centrifugal* method of budding; in *Montipora* an undifferentiated apex of coenenchyma takes the lead in the growth (as may be well seen in both the widely different species *M. foliosa*, Pallas, and *digitata*, Dana), and new calices originate in this coenenchyma *above* the already formed calices; in other words, the budding is *centripetal*. This distinction lies so deeply rooted in the structure and physiology of these corals that it is difficult to see how a directly "connecting-link" between the two types can be found. I should rather expect to find the connecting-point far back in some common form in remote geological time.

The distinction is the same as that denoted in flowering plants by the terms "determinate" and "indeterminate inflorescence." In a determinate inflorescence growth is centrifugal, the first flower being formed at the apex; in an indeterminate inflorescence the first flowers are formed at the sides and they successively *approach* the centre or apex of the spike. The distinction appears to me to furnish a good character by which to divide the Madreporinæ from the Montiporinæ (sufficiently closely allied to each other and removed from the Poritidæ, as it seems to me, by the possession of a spongy coenenchyma, of a well-developed and deep calicle, devoid of columella and pali); hence I would classify Madreporidæ as follows:—

Subfam. 1. *Madreporinæ*.—Gemmation centrifugal, from the sides of terminal calices.

Subfam. 2. *Montiporinæ*.—Gemmation centripetal, from a terminal coenenchymal mass.

A new genus, which I describe below under the name *Ana-*

cropora, referable, from the character of its budding, to the subfamily Montiporinæ, fully bears out these views as to the nature and importance of the mode of gemmation occurring in that subfamily.

ANACROPORA *, n. gen.

Madreporidæ of ramosse habit. Axis and apex of branches formed by a spongy cœenchyma. New calicles formed centripetally, *i. e.* from the base towards the apex; no calicle of any kind at the apex. Calicles equally distributed all round stem and branches, with a tendency to an arrangement in longitudinal series. Septal system well developed, comprising two cycles of six septa each, two (approximately upper and lower) primaries being larger than the four lateral primaries.

Obs.—*Anacropora* is based on the new species *A. Forbesi*, described below, and on some forms which occur in the 'Challenger' collection of reef-corals, to be hereafter described by Mr. J. J. Quelch, of the Natural-History Museum; I have had the advantage of Prof. Duncan's and Mr. Quelch's opinions on this important form, opinions which have been freely and kindly given. The general growth and other characters given above are essentially the same in all the species. In all the growth is low, the branches tending to form inosculations between each other; the stem and branches are cylindrical, and no distinct tubular calicles are formed.

From *Madrepora* this genus differs markedly in the centripetal production of the calicles, by which the youngest calicles are always the uppermost. From the subgenus *Isopora*, Studer (see above), it differs in the same point, as well as in its slender dendroid growth; but the first distinction is not so marked at first sight, since the peculiar growth of *Isopora* almost necessitates the absence of a *distinct* apical calicle, but (as stated above) the mode of gemmation is centrifugal in *Isopora*, as in *Madrepora* s. str. Other points distinguishing *Anacropora* from most species of *Madrepora* are the formation of the axis of the branches by a spongy cœenchyma, whereas in many (if not all) *Madreporæ* this, in accordance with the centrifugal habit of budding, is occupied to a greater or less distance from the ends of the branches by the downward prolongations of the septa and the interseptal spaces of the apical calicle. The rudimentary condition of the external part of the calicle distinguishes *Anacropora*; for although it is

* From *ἀν*, privative particle, *ἄκρος*, summit, *πόρος*, passage or pore; in allusion to the absence of pores from the ends of the branches.

commonly found (I refer to the sunk calicles occurring in so many species between the prolonged tubular or nariform ones) in *some*, it is never, so far as my knowledge extends, found in *all* the calicles in any *Madrepora*.

Although in its general appearance it differs remarkably from even the branched species of *Montipora*, yet the structural differences which separate *Anacropora* from this genus are very far less distinctive than those which separate it from *Madrepora*. In the first place, in spite of its external resemblance to *Madrepora*, it has the same system of calicular budding (viz. centripetal, from the distal coenenchyma) which we find well developed in the ramose *Montipora*; the trabecular structure and the two-cycled arrangement of the septa is the same in both genera. On the other hand, whereas in *Anacropora* there is always an undifferentiated coenenchymal apex, devoid of calicles, to the branches, in *Montipora* this apex appears always to bear at least one calicle on its surface. In *Anacropora* the calicles are always rather distant and tend to form lines, and are slightly raised above the surface, forming low hill-like eminences, whereas in the ramose *Montipora* (e. g. *digitata*, Dana, *divaricata* and *superficialis*, Brüggeman), which on the whole most closely approach *Anacropora*, the calicles open flush with the surface, are crowded indiscriminately, and no linear arrangement is apparent. In *Montipora foliosa*, it is true, the calicles, especially on the posterior aspect of the corallum, are elevated in a similar manner; but the foliate growth and the monticular *inter-calicular* eminences of the upper surface seem to remove this species far from the ramose *Montipora*. It seems to me not improbable that, for the reasons I have indicated, these ramose forms may have to be separated from the foliate and massive species of *Montipora*.

The relations of *Anacropora* may be thus shortly stated:—*Anacropora* has the general growth of *Madrepora*, but the manner of budding of *Montipora*.

The following is a description of the single species referable to this genus which I am able to describe; owing to the interest attaching to the type, I have allowed myself to give its characters at full length:—

Anacropora Forbesi, n. sp. (Pl. XI.)

Corallum branching frequently, dichotomously, occasionally subtrichotomously; branches given off in succession in a subspiral manner, the planes of successive bifurcations varying from about 30° to 100° with regard to each other; angle between branches composing bifurcation 80° to 100°. Stem and branches slightly curved, the apical branches more strongly

so, cylindrical, except the terminal branches, which tend to curve outwards and taper gradually to points; diameter, main axes 6-7 millim., intermediate and terminal branches about 4 millim., greatest length between bifurcations of main branches about 30 millim., terminal twigs 25 millim. long. Calicles arranged more or less definitely, for the most part in series which follow approximately the longitudinal axis of the stem and branches, the calicles of one series alternating with those of the adjacent series; series about 2 millim. apart, calicles about 2 to 2.5 millim. apart in the series. Calicles forming, everywhere but on the tips of the branches, low rounded elevations, by the gradual rising of the surface towards their inferior margins to a height of .25 to .7 millim., and occasionally by the similar but very slight elevation of their superior margins. Calicles orbicular, looking upwards; orifice of adult calicles .5 to .7 millim. in diameter; on the tips of the branches they open on the level of the surface of the corallum, are more or less imperfectly defined from the surrounding loose cœnenchyma, and measure about .25 to .4 millim. in diameter. Septa trabecular, consisting of vertical series of horizontal pointed projections from the wall of the calicle, beginning just below its margin, distinct. Primaries about .25 millim. in length in full-grown calicles, comprising two main, opposite ones, variously placed (*i. e.* from parallel to the long axis to at an angle of 45° with the same), which converge towards the bottom of the calicle, where they meet and form a vertical plate; the other primaries are slightly smaller and do not meet below. Secondaries varying from about half the diameter of primaries to mere points on the side of the calicle; the secondary septum between the two lateral primaries is sometimes wanting.

Corallum slightly vermiculate, always covered by minute points at surface (at apex looser, very porous); the outer one-quarter of diameter (except at apex, see fig. 5), formed of a denser tissue, in which the calcareous trabeculæ exceed in diameter the spaces between them; the central one-half of the diameter (*viz.* usually about 2 millim.), consisting of a loose tissue, in which the calcareous bars are only about half the diameter of the intervening spaces; the meshes of this tissue (as seen in transverse section of a branch) elongate towards margin, smaller and relatively shorter at centre. Apices of branches, to a distance of from 2-8 millim. from the ends (see fig. 5), formed of the looser axial cœnenchyma, and carrying more or less rudimentary calicles, which are at least 1 millim. from all other calicles in the same longitudinal series.

Hab. Keeling Islands, Indian Ocean; deeper water inside reef.

Represented by a single colony (fig. 1) and a detached branch, which has lived independently after its fracture from the parent specimen. They were collected and presented to the British Museum by Mr. H. O. Forbes, F.Z.S. &c., who has already (Proc. Roy. Geogr. Soc., Dec. 1879) described these islands, and with whose name I have much pleasure in associating this new type. The chief colony measures 83 millim. ($3\frac{1}{2}$ inches) in height, 100 millim. (4 inches) in greatest breadth, and 55 millim. ($2\frac{1}{4}$ inches) from front to back; the detached branch, which bifurcates three times, was about 60 millim. long when alive. Parts of the corallum, owing either to an evanescent pigment or to traces of animal matter, have a most delicate pink tint.

Some interesting points are brought out by the detached branch; this occurs unrooted, but obviously had been broken off from the colony while yet alive (see fig. 4) and lived subsequently free. As commonly happens in such cases, the fractured surface has healed over; but in this case the new material is not a continuation of the *superficial* cœnenchyma of the adjacent side over the stump, but the prolongation outwards of the loose central cœnenchyma which has developed on itself five or six young calicles. Here also the law of centripetal gemmation asserts itself, these calicles occurring on the sides of a central cone of loose cœnenchyma, of which the apex, 1 millim. long, is undifferentiated and bears no calicles. The same law is followed in the process of repair exhibited by a broken stump of a branch on the larger specimen. The wide angle of bifurcation of the branches causes the colony to assume a low decumbent form, and bringing, as it does, neighbouring branches into juxtaposition, gives rise to anastomoses; the branching in various planes gives it a broad top.

Bilateral Symmetry in the Madreporidæ.—In *Madrepora elegans* we have a decided bilaterality in the arrangement of the calicles on the corallum, a circumstance which has induced MM. Milne-Edwards and Haime to entertain the idea that this form might be generically distinct from *Madrepora*. No other Madreporidæ exhibit this, so far as I am aware; bilaterality in the arrangement of the parts of the calicle is, however, a prominent feature of a number of *Madreporæ*, taking the form of a superior development of the upper and lower (distal and proximal) primary septa, sometimes carried to the extent of their union in the middle line at no great distance below their upper margins. In *Montipora* also (at any rate, in *digitata*, Dana) the primaries are thus distinguished; but here they are not always strictly upper and lower in relation to the long axis of the branches. This form of calicular bilaterality

is well marked also in *Anacropora*, although I have not observed it to extend to the union near the summit of the calicle of the two leading septa; in this genus also these two septa are sometimes placed diagonally with relation to the axes of the branch (see fig. 2). Klunzinger (Kor. roth. Meer. ii. p. 2) states that in *Madrepore* one of these two (which he calls "Hauptsepta") has its corresponding tentacle longer than the other eleven tentacles.

In *Seriatopora* these two septa are represented *in position* by the long plate which extends from the proximal to the distal wall of the calicle, *i. e.* in the direction of its (here) longer axis; but the fact that, as Prof. Moseley has shown (Quart. Journ. Microsc. Sci. n. s. xxii. p. 392), six primary septa are present without counting this, seems to favour Milne-Edwards and Haime's view, that this plate is columellar, not septal, in origin—in which case *Seriatopora* would differ from the Madreporidæ in having its primary septa wholly distributed to the right and left of a dorso-ventral line.

Budding or Fission in Madrepore?—Prof. Studer, in his paper on Budding and Fission in the Madreporaria (Mitth. naturf. Ges. Bern, 1880, p. 3), surmises (p. 14) from appearances that in the Madreporidæ (he evidently refers only to *Madrepore*, as *Montipora* has no apical calicle) the new calicles are really formed by fission or lateral gemmation from the margin of the apical calicle, which he thinks sends out curved bulges from its margin. All the evidence I have gathered myself from *Madrepore* is rather in favour of the old view that the buds are formed from the sides of the wall of the apical calicle in this genus.

EXPLANATION OF PLATE XI.

- Fig. 1.* *Anacropora Forbesi*, the chief specimen, seen somewhat from above. Natural size.
- Fig. 2.* Ditto, part of a main branch of the same specimen, showing characters of adult calicles and of the exterior of the cœnenchyma. $\times 6$ diameters.
(Note that one calicle has the main primary septa dorso-ventral, the other diagonal in position.)
- Fig. 3.* Ditto, vertical section of main branch of the same specimen, showing:—*a*, axial; *b*, superficial cœnenchyma; and *c*, longitudinal section of a calicle. $\times 6$ diameters.
- Fig. 4.* Ditto, basal end of detached branch, showing the renovation of the stump by the emergence of the loose axial cœnenchyma and the formation in this cœnenchyma of young calicles. $\times 3$ diameters.
- Fig. 5.* Ditto, apex of branch of chief specimen, showing the loose texture of the cœnenchyma at this point and the formation (as in fig. 4) of young calicles from this loose cœnenchyma. The view selected shows an unusually regular longitudinal series of young calicles. $\times 3$ diameters.